ASSESSING EDGE AVOIDANCE AND AREA SENSITIVITY OF RED-EYED VIREOS IN SOUTHCENTRAL ONTARIO

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ABSTRACT.—We assessed edge avoidance, area sensitivity, and the relationship between local and regional forest cover for nesting Red-eyed Vireos (*Vireo olivaceus*) in 13 forest fragments (1–2,353 ha in size) in southcentral Ontario, Canada. Red-eyed Vireo territories and nests were not significantly farther from the edge than random points in any of the forest fragments, and there was no relationship between the probability of a male pairing and the distance of the territory from the edge of the forest fragment. The density of singing males and the probability of a male being paired increased significantly with increasing local forest cover within a 2-km radius of a study site, but not with forest fragment area or regional forest cover within a 10-km radius. Nest success was low and the probability of a nest being parasitized by the Brown-headed Cowbird (*Molothrus ater*) or successfully fledging \geq 1 host young did not vary with distance of the nest from the forest edge or with any of our area or forest cover measures. Red-eyed Vireos did not display edge avoidance nor did they appear to be area sensitive within our study region, but there was a positive relationship with the amount of local (2-km radius) forest cover. Maintaining localized regions with high forest cover has been recommended on numerous occasions for the conservation of area sensitive. *Received 22 May 2001, accepted 17 April 2002.*

The Red-eyed Vireo (Vireo olivaceus) is a forest-dwelling Neotropical migrant songbird that breeds within deciduous and mixed forests throughout much of North America. At present, conclusions concerning the habitat requirements of this species are contradictory, particularly in regard to forest edge avoidance and minimum habitat requirements. Although not considered to be in decline (Sauer et al. 2001), habitat requirements of any species should be known before population declines are evident as the appropriate classification can influence future management of the species. Recent studies variously suggest that the Red-eyed Vireo avoids forest edges (reviewed in Villard 1998) or is an interior-edge generalist with extremely plastic habitat use, including wooded suburbs, fence rows, and forest edges (James 1976, Whitcomb et al. 1981). Most, but not all, studies suggest that the species is area sensitive (reviewed in Freemark and Collins 1992). None of the studies upon which these classifications are based include data from nest sites or reproductive success.

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Edge avoidance has been defined by lower occurrences of territories and nests along the edge of a forest fragment than in the forest interior (King et al. 1997, Villard 1998). An area sensitive species is one that occurs more frequently, or increases in density, as fragment area increases (Freemark and Collins 1992). Area sensitive species should thus show positive relationships between the density of singing males and the area of forest fragments. Species with the greatest area sensitivity are presumed to show positive relationships between forest fragment area and male density, pairing success, and nesting success (e.g., Ovenbirds, Seiurus aurocapillus; Robinson et al. 1995, Burke and Nol 1998), so that the productivity (number of fledged young produced per ha of forest) of a forest fragment is very strongly influenced by forest fragment area. Recent studies also indicate that many forest bird species experience reduced density, pairing success, and nesting success in forest fragments embedded in regions with low forest cover (Robinson et al. 1995, Mazerolle and Villard 1999). Thus, forest habitat loss should negatively impact: (1) species that avoid forest edges, (2) species that are area sensitive, and (3) species that respond negatively to reduced amounts of forest cover. Establishing the appropriate classification for the Red-eyed Vireo (and other forest bird species) will help direct land use planning and forest conservation strategies.

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In this study, we tested whether Red-eyed Vireos nesting in forest fragments in deciduous woodlands of southcentral Ontario avoid edges, and whether male density, pairing success, and nesting success vary in relation to fragment size. Given the flexibility in habitat preferences reported for this species (James 1976) but the general restriction to wooded areas, we tested whether Red-eyed Vireos respond more strongly to forest cover or forest fragment area by determining which is the better predictor of male density, pairing success, and nesting success in our study area.

METHODS

Study area.—We conducted the study in eight forest fragments during 1997 and five during 1998, all situated in the Great Lakes-St. Lawrence Lowlands of southcentral Ontario, Canada (Hills 1959) near Peterborough, Ontario (44° 18' N, 78° 19' W). We selected fragments of upland deciduous forest to represent a wide range of fragment areas (1–2,352 ha). The surrounding landscape consisted of agriculture and rural low density housing (0–3 houses around the fragment perimeter).

Study plots, ranging from the entire forest in smaller fragments to 4-ha plots, were located within relatively mature (>40 years) deciduous, closed canopy forest. Plots within larger fragments were square in shape, with one edge located near the forest edge to allow comparison with small forest fragments. The vegetation of all study sites was dominated by mature sugar maple (*Acer saccharum*), but also included American beech (*Fagus grandifolia*), ironwood (*Ostrya virginiana*), and white ash (*Fraxinus americana*); less abundant canopy species included eastern hemlock (*Tsuga canadensis*), white elm (*Ulmus americana*), and white pine (*Pinus strobus*; Burke and Nol 2000).

We assessed the degree of habitat loss from fragment area and by three scales of forest cover: 2-km radius (1,260 ha), 5-km radius (7,850 ha), and 10-km radius (31,420 ha). Multiple scales were considered to gain a better understanding of the relationship between Red-eyed Vireo reproductive success and the amount of forested area in a region. We measured the surrounding forest cover from the center of the fragment using forest cover maps derived from LANDSAT imagery taken in 1984 and 1985 (Hounsell et al. 1992) and digitizing software. The area of the study fragment was excluded when measuring forest cover in order to reduce correlation between fragment area and surrounding forest cover.

Edge avoidance.—We assessed whether Red-eyed Vireos were avoiding edges by measuring the distance to the nearest nonforest edge from territories and nests, and comparing these to distances to the edge from randomly selected points within each forest fragment. We defined forest edge as any break in the canopy with a diameter \geq 3 times the canopy height (Paton 1994). The

distance from a territory to the nearest edge was measured from a song perch where a male had been observed singing. The number of random points per fragment varied from two in the smallest fragments to five (58 total). We analyzed these data using analysis of covariance (ANCOVA) with fragment size as the covariate and site (territory or nest versus random points) as the class variable. This design allows for a test of differences in the distance from territories and nests to the forest edge in comparison to the distance to the edge from random points while controlling for inherent differences in the distance to the edge as a function of fragment area (PROC GLM; SAS Institute, Inc. 1990). Fragment size and distance to the edge were log transformed to conform to the assumptions of ANCOVA.

Area sensitivity.—We determined the density of male Red-eyed Vireos within each fragment by spot mapping from early June to early July each year. Each fragment was visited 2–3 times per week during early morning and the locations of singing males were recorded. In larger fragments, not all territories occurred completely within the bounds of the plot. Males with the majority of a territory within the plot were given a value of 0.5 territory whereas birds with the majority of a territory occurring outside the plot were not included (Villard et al. 1993). We compared male density across the continuum of fragment sizes and forest cover measures using multiple regression (PROC GLM; SAS Institute, Inc. 1990).

To determine pairing success, we observed individual Red-eyed Vireo males throughout June and July. Mating status was determined by one or a combination of several criteria (Villard et al. 1993). Since male and female Red-eyed Vireos are not sexually dimorphic in appearance, we considered males to be paired if they were engaged in nonaggressive interactions with another bird of the same species. We also considered males paired if we observed them carrying food or feeding fledglings, or if we found an active nest within a territory. Gibbs and Faaborg (1990) and Villard et al. (1993) both suggested 90 min of total observation time is needed to conclude that ground nesting birds are not paired. However, because male Red-eyed Vireos were difficult to observe in the canopy, we extended this time; we visited each male repeatedly over the study period until there was positive proof of pairing or until approximately 120 min of total observation time had elapsed, at which time we assumed the bird was not paired. Each observation session continued until visual or auditory contact had ceased for ≥ 5 min.

We found nests by observing adult birds fly to the nest as well as systematically searching the foliage within territories. As nests situated on higher branches were more difficult to observe, it is possible that there was a bias toward finding lower nests. We checked each nest every 3–5 days and recorded nest contents. We considered a nest successful if ≥ 1 young of the host species fledged, and failed if no young of the host species fledged. We considered failed nests depredated if the nest structure, eggs, or nestlings disappeared, or parasitized if no host young fledged although Brown-



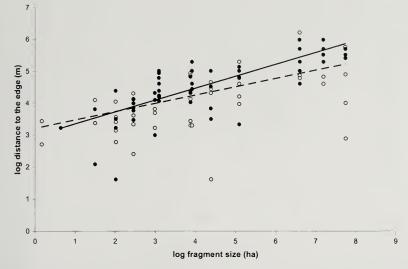


FIG. 1. Distance to the nearest nonforested edge from male Red-eyed Vireo territories (solid circles and solid line) and randomly located points (open circles and dashed line) across a continuum of fragment sizes for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

headed Cowbird (*Molothrus ater*) young may have fledged successfully. As most parasitized nests successfully fledged host and cowbird young, we determined the proportion of nests containing cowbird eggs or young (parasitism rate).

We analyzed pairing and nesting success as a function of fragment size and forest cover measures using logistic regression (PROC LOGISTIC; SAS Institute, Inc. 1990). Distance from the edge was analyzed in separate logistic regressions to determine whether there was a significant relationship with the probability of pairing or nesting successfully. Logistic regression calculates the probability of obtaining a "success" as predicted by the independent variables (Manly 1994). Thus, each male Red-eyed Vireo was considered individually and defined as successful if paired. The probabilities of nest success, predation, and parasitism also were analyzed in this manner. Because forest fragments, rather than individual birds or nests, were the appropriate sample units, the dependent variable was considered as the proportion of successes to the total number in each fragment (events/trial syntax in the MODEL statement; SAS Institute, Inc. 1990:1079). All independent variables were log transformed to conform to the assumptions of logistic regression.

RESULTS

Data from 1997 and 1998 were combined because there were no significant differences between years in male densities (*t*-test: $t_{11} =$ 1.08, P = 0.30), pairing success ($t_{11} =$ 1.86, P = 0.090), or nesting success ($t_6 = 0.74$, P =0.48). Forest cover within 2 km and 5 km were highly correlated (r = 0.73, P = 0.003) as was forest cover within 5 km and 10 km (r = 0.87, P < 0.0001) so we used only the 2 km (hereafter "local forest cover") and 10 km (hereafter "regional forest cover") measures of forest cover in the analyses (r = 0.52, P = 0.070). Forest fragment area was not correlated with either local (r = 0.42, P = 0.15) or regional (r = 0.19, P = 0.52) forest cover.

Edge avoidance.-We measured the distance to the nearest forest edge from 62 Redeyed Vireo territories, 36 nests, and 58 randomly selected points. The overall model comparing the distance of territories and random sites was significant (ANCOVA: r^2 = $0.47, F_{3.116} = 34.19, P = 0.0001, n = 13$ fragments). The significance of the model was driven by greater distances to the edge in larger forest fragments (size effect: $F_{1,116} = 94.55$, P = 0.001), as there was no trend for territories to be farther from the edge than random points (site effect: $F_{1,116} = 0.53$, P = 0.47; size × site interaction: $F_{1,116} = 2.89, P = 0.092;$ Fig. 1). The overall model comparing distance to the edge from nests and random points was significant (ANCOVA: $r^2 = 0.15$, $F_{3,70} = 4.12$, P = 0.010, n = 8 fragments). Again, distances to the edge were greater in larger forest fragments and were not farther from the edge than randomly selected points (size effect: $F_{1.70} =$ 11.97, P = 0.0009; site effect: $F_{1,70} = 1.64$, P

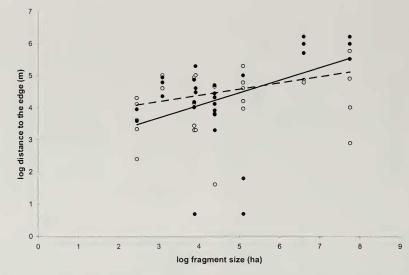


FIG. 2. Distance to the nearest nonforested edge from Red-eyed Vireo nests (solid circles and solid line) and randomly located points (open circles and dashed line) across a continuum of fragment sizes for eight forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

= 0.20; fragment × site interaction: $F_{1.70}$ = 1.36, P = 0.25; Fig. 2). Before log transformation, the variability (SE) in distance to the nearest nonforest edge of territories, nests, and random points all increased significantly with forest fragment size (linear regression; territory: r_2 = 0.68, $F_{1.11}$ = 26.22, P = 0.0007; nest: r_2 = 0.77, $F_{1.6}$ = 25.07, P = 0.002; random: r^2 = 0.39, $F_{1.11}$ = 7.1, P = 0.015).

Area sensitivity.—Sites ranged in percent forested area from 11–94.3% at the local (2km radius) forest cover scale and from 13.5– 53.2% at the regional (10-km radius) forest cover scale. Red-eyed Vireos occurred in all 13 forest fragments, ranging in density from 0.7–4.7 males/ha. The overall regression model for predicting the density of male Red-eyed Vireos was significant ($r^2 = 0.37$, $F_{3,9} = 3.34$, P = 0.050). Density increased significantly as a function of local forest cover (Fig. 3), but did not vary significantly with either fragment area or regional forest cover (Table 1).

We determined pairing success for 79 male Red-eyed Vireos: 46 (58.2%) were paired. Local forest cover was the only independent variable to enter significantly into the logistic regression model, indicating it was the best predictor of any individual male Red-eyed Vireo successfully attracting a mate (Table 2; Fig. 4). There was a significant positive correlation between density and pairing success (r = 0.8, P = 0.0006, n = 13 fragments).

Red-eyed Vireos build a hanging cup nest suspended from the fork of a small branch, ranging from 0.5–21 m in height but typically located from 2-4 m (Peck and James 1987). A total of 47 nests was found in eight forest fragments during the two years; 19 (40.4%) successfully fledged ≥ 1 host young. Neither forest area, local forest cover, regional forest cover, nor distance of the nest to the edge significantly affected the probability of nesting successfully (Table 2). Predation accounted for the majority of nest failures, with 25 nests (53.2%) depredated. Again, none of the independent variables significantly predicted the probability of nest predation (Table 2). Nest failure due to parasitism was low, as only three (6%) of the nests fledged only Brownheaded Cowbird young. Despite few total nest failures due to parasitism, the parasitism rate was high with 12 nests (25.5%) partially parasitized, although none of the independent variables significantly explained the pattern of nest parasitism (Table 2). Only seven of 47 nests (14.9%) escaped predation or parasitism.

DISCUSSION

Our results indicate that Red-eyed Vireos did not avoid forest edges for establishing ter-

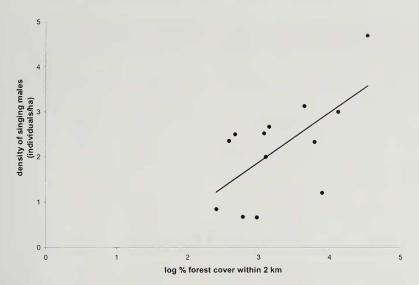


FIG. 3. Male Red-eyed Vireo density and the percent of forested habitat within a 2-km radius for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

ritories or for nesting, and they were not an area sensitive species within our study region. Male density and pairing success increased only in relation to increasing forest cover within a 2-km radius of a study site, indicating that this species is not sensitive to fragment area but may be sensitive to the total amount of forest area within a relatively localized landscape context. However, the relationship between density and local forest cover appeared to be largely driven by one forest fragment with high local forest cover and high Red-eyed Vireo density (Fig. 3). Regardless of this uncertainty, these results help to clarify habitat associations of this species by offering evidence that they are neither edge avoiding nor area sensitive. This may explain why Redeyed Vireos are one of the few Neotropical migrants to nest regularly in heavily wooded suburban areas and city parks (Peck and

TABLE 1. Parameter estimates from multiple regression analysis of male Red-eyed Vireo density during the 1997 and 1998 breeding seasons in 13 forest fragments in southcentral Ontario, Canada.

Parameter	Slope	SE	t	Р
Intercept	0.97	5.96	0.163	0.87
Fragment area	-0.16	0.176	0.91	0.38
Local forest cover	2.00	0.725	2.76	0.022
Regional forest cover	-1.04	0.822	1.33	0.22

James 1987). Fragment occupancy by female and, perhaps less certainly, male Red-eyed Vireos appeared to be associated with the surrounding landscape context and not merely fragment area. This supports the findings of Villard et al. (1995) for some other Neotropical migrant bird species.

Our results, based on territory and nest locations as well as patterns of density and pairing success relative to forest edges, support the classification of the Red-eyed Vireo as an interior-edge generalist species rather than an edge avoiding species. The density of interioredge generalists should not be related to fragment area, in contrast to forest interior species (Bender et al. 1998), as they are able to use edge habitat which comprises a greater proportion of small forest fragments. Although the mean distance to the forest edge from both territories and nests increased with fragment area, there was no evidence that Red-eyed Vireos actually were selecting interior territory or nest sites in preference to edge sites in larger fragments. The increased variability of territory and nest placement in larger forest fragments indicates that this species utilizes both edge and interior habitats even when large amounts of interior habitat are available, which supports the conclusion of plasticity in habitat requirements. Nesting habitat does not appear to be a limiting factor for Red-eyed

Variable	п	Parameter	Coefficient	SE	x ²	Р
Pairing success	13					
		Intercept	-10.41	5.20	4.01	0.04
		Fragment area	-0.26	0.19	1.81	0.18
		Local forest cover	2.22	0.87	6.55	0.01
		Regional forest cover	-0.15	0.70	0.05	0.83
		Distance to the edge	0.17	0.27	0.82	0.54
Nesting success	8	0				
		Intercept	1.18	5.50	0.04	0.83
		Fragment area	-1.13	0.25	0.26	0.61
		Local forest cover	0.76	0.66	1.34	0.25
		Regional forest cover	-0.62	0.77	0.65	0.42
		Distance to the edge	0.084	0.24	0.11	0.72
Nest predation	8	5				
		Intercept	-7.71	5.65	1.86	0.17
		Fragment area	-0.23	0.28	0.71	0.39
		Local forest cover	-0.33	0.69	0.23	0.62
		Regional forest cover	1.11	0.78	2.01	0.15
		Distance to the edge	-0.10	0.24	0.18	0.67
Brood Parasitism	8	5				
		Intercept	3.71	6.04	0.38	0.54
		Fragment area	-0.53	0.41	1.67	0.19
		Local forest cover	0.09	0.77	0.01	0.89
		Regional forest cover	-0.35	0.88	0.16	0.67
		Distance to the edge	-0.69	0.31	1.04	0.30

TABLE 2. Parameter estimates from logistic regression analysis of four measures of Red-eyed Vireo reproductive success during the 1997 and 1998 breeding seasons in southcentral Ontario, Canada. N is the number of forest fragments studied.

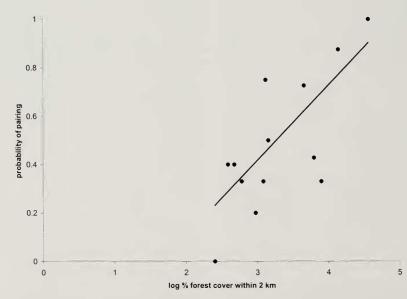


FIG. 4. Probability of a male Red-eyed Vireo pairing and the percent of forested habitat within a 2-km radius for 13 forest fragments in southcentral Ontario, Canada, during the 1996 and 1997 breeding seasons.

Vireos in small forest fragments within this part of southcentral Ontario.

In comparison to other forest bird species monitored within our study sites (Burke and Nol 2000), the rates of predation and parasitism on Red-eyed Vireo nests were high. The fate of Red-eyed Vireo nests did not vary with fragment area, forest cover, or distance from the nest to the edge. Although these results are based on a small sample of forest fragments, they are consistent with research based on a larger sample size conducted in our study region (Burke and Nol 2000). Our estimate of nest success may have been lower than that of the entire population because we monitored only nests that were <4 m high. Red-eyed Vireos can nest in the subcanopy and canopy of hardwood forests (Peck and James 1987) and these nests may, in general, avoid predation, since shrub nests have been identified as the most vulnerable to predators (Sargent et al. 1998). Locating and monitoring these high nests may provide a more accurate measure of nest success for this species.

The detection of edge effects on forest bird nest predation rates is common in forest fragments embedded in agricultural landscapes (reviewed in Paton 1994, Andren 1995), such as southcentral Ontario. However, composition of the local predator community is important to understanding the spatial pattern of nest predation (Andren 1995), as some studies have found that predation on birds' nests by avian predators is higher at forest edges and in small forest fragments while predation by small mammals is higher in forest interiors and larger fragments (Nour et al. 1993, Haskell 1995). We did not identify nest predators in our study and in combining all predation events may have masked trends in distance to the edge, fragment size, or forest cover by different types of predators.

Estimates of pairing success and, less certainly, density seem to indicate that Red-eyed Vireos preferred forest fragments embedded in areas of high forest cover, even though there did not appear to be any fitness consequences (increased nest success) in this preference. It is possible that our sample size of nests did not have the power to detect such relationships.

Although currently not a species of conservation concern, Red-eyed Vireos appear to occur at lower density and be less successful in attracting mates within regions of low local forest cover. It is therefore possible that if deforestation continues, populations of this species could begin to decline. This result supports the findings of Trzcinski et al. (1999) that habitat loss (decrease in forest cover) may be the most important factor affecting the distribution of forest breeding birds. Maintaining localized regions with high forest cover (>30%) has been recommended on numerous occasions for the conservation of area sensitive forest birds (Robbins et al. 1989, Freemark and Collins 1992, Freemark et al. 1995); our results suggest high forest cover also may benefit species that do not appear to be area sensitive. Large forest fragments often are embedded in landscapes with high forest cover, thus preserving these landscapes also would benefit both interior nesting species and interior-edge generalists.

ACKNOWLEDGMENTS

We thank the Richard Ivey Foundation and the Biology Dept. of Trent Univ. for funding the research. We also thank R. McGhie and anonymous reviewers for their comments on earlier drafts of the manuscript.

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